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EFFECTS OF BROWSING PREDATORS: ACTIVITY CHANGES IN INFAUNA FOLLOWING TISSUE LOSS

SARAH ANN WOODIN

Department of Biology and Belle W. Baruch Institute of Marine Biology and Coastal Research, University of South Carolina, Columbia, South Carolina 29208

Abstract

Effects of tissue loss on defecation and/or tube building are documented for three infaunal species of polychaete annelids, *Abarenicola pacifica, Axiothella rubrocincta,* and *Spiophanes bombyx. Abarenicola* and *Axiothella* feed head down and expose their tails while defecating; their tail tips were experimentally ablated. *Spiophanes* feeds on the sediment surface with its pair of tentacles and its head. One or both of its tentacles were experimentally removed. The tissues removed in the experiments are those often lost to browsing predators in field populations. Defecation frequency and amount were significantly reduced in the experimental individuals relative to controls in all three species. In *Spiophanes* tube building was also significantly reduced; in *Axiothella* it was not. These results indicate that rates of biogenic sediment modification can be strongly affected by tissue losses of infauna to browsing predators.

Introduction

Tissue loss to browsing predators occurs commonly in plants (Harper, 1977; Grime, 1979) as well as animals. In marine sedimentary environments primary components of the diets of juvenile flatfish are the tails of arenicolid polychaetes and the siphons of tellinid bivalves (Macer, 1967; Edwards and Steele, 1968; Kuipers, 1973, 1977; deVlas, 1979a). In such habitats a significant percentage of the infauna preyed upon by browsing predators are usually regenerating body parts (Mangum, 1964; Ronan, 1975; deVlas, 1979b; Woodin, 1982). A variety of body parts are lost to such predators, especially those parts exposed to predatous risk above the sediment surface. Arenicolid and maldanid polychaetes, which usually live head downward and expose their tails to defecate, lose their tails (Mangum, 1964; deVlas, 1979b). Maldanids also lose their heads occasionally but whether this is due to a subsurface predator or to the maldanid exposing its head on the sediment surface is unknown (Wilson, 1979). Individuals which expose appendages or heads to feed are often found regenerating those parts (*e.g.,* sabellid polychaetes: Berrill, 1931; tellinid bivalves: Trevallion *et al.,* 1970; phoronid worms: Ronan, 1975; ophiuroids: Sides, 1981; spionid polychaetes: Woodin, 1982; venerid bivalves: Peterson and Quammen, 1982). Tissue loss appears to be a common occurrence at least for organisms which feed or defecate on the sediment surface.

In sedimentary habitats the infauna affect the survivorship and growth of one another by both indirect and direct interactions. The indirect interactions often occur via sediment modification (see reviews in Rhoads, 1974; Woodin and Jackson, 1979; Rhoads and Boyer, 1982; Thayer, 1983; Woodin, 1983). Defecation by organisms can modify sediments. The effects on the surrounding organisms are functions of the frequency of defecation and the amount per feculence (Brenchley, 1981). Any event that significantly affects the defecation rates will therefore indirectly affect growth and survivorship of other individuals.

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Given the apparent frequency of tissue loss, it is of interest to ask two questions. One, how do the activities of individuals suffering tissue loss differ from those of intact individuals? Two, how long is this activity difference maintained? This paper documents changes in activity resulting from tissue loss in three common polychaete families, the Arenicolidae, the Maldanidae, and the Spionidae, all of which frequently suffer tissue loss in the field.

Materials and Methods

The following infaunal species were used in the experiments:

1. *Abarenicola pacifica* Healy and Wells, an arenicolid polychaete, lives head down in a J- or L-shaped burrow. It exposes its tail to defecate and leaves obvious spiral fecal castings on the sediment surface (Hobson, 1967). Size 54 to 75 mm (Hartman, 1969).
2. *Axiothella rubrocincta* (Johnson), a maldanid polychaete, lives head down in a vertical tube (see Kudenov, 1982 for a contrasting life style). It exposes its tail to defecate. Its feces are usually a fine layer spewed out onto the sediment surface. Size 70 to 120 mm but up to 200 mm (Hartman, 1969).
3. *Spiophanes bombyx* (Claparede), a spionid polychaete, lives head up in a tube. It exposes its pair of tentacles and sometimes its head to feed (Woodin, 1982). Its feces are deposited onto the sediment surface in long consolidated rods. Size 25 to 60 mm (Light, 1978).
4. *Pygospio elegans* Claparede, a spionid polychaete, lives head up in a tube. It exposes its pair of tentacles and head to feed and has fecal rods similar to those of *Spiophanes* (Woodin, 1982). Size 10 to 15 mm (Light, 1978).

In all of the experiments field collected animals were placed in cores of azoic sediment, and the activity rates of ablated individuals were compared to those of control individuals. For these experiments defecation and tube-building, both known to affect sediment properties, were measured (Table I). In all but one experiment one or more measurements were made of defecation activity and animals were monitored to determine when they resumed defecation. For species that build tubes, tubes in the sediment at termination were collected and weighed as an additional measure of activity (Table I).

All animals were used within 48 hours of collection. Damaged or regenerating individuals were rejected. The sediment for the experiments was collected from the same locale as the animals. The sediments were either treated with freshwater for 72 hours (*Abarenicola* experiments) or frozen for a minimum of 48 hours (all other experiments). The sediments were then flushed with sea water and sieved through a 0.5 mm mesh sieve in sea water to remove all large material. The cores were filled with sediment and placed in a sea water tank with running sea water for 24 hours before the experimental animals were added. Prior to addition of the animals, the tank was drained and refilled. Sediment samples for determination of organic carbon were taken at initiation and termination of each experiment. The samples were dried to constant weight at 80°C and then ashed at 500°C for four hours.

Abarenicola *experiments*

Abarenicola pacifica were collected in March 1979 from a muddy sandflat at False Bay, San Juan Island, Washington state (48°29'N:123°04'W). Individuals were cleaned of sediment and sorted into size groups. Individuals used in the experiment had a mean length of 3.2 cm (S.D. = 0.5, n = 80).

TABLE I

Summary of activity measurements for each experiment; all measurements were made in the laboratory unless otherwise indicated

1. Number of seconds from placing the individual on the sediment surface to complete burial was recorded at initiation of the experiment.
   Abarenicola (field and laboratory)
2. Individuals were monitored to determine when they resumed defecation after initiation of the experiment.
   Abarenicola (field and laboratory), *Axiothella, Spiophanes*
3. Individuals were observed for set time periods to determine number and/or amount of defecation(s) per time interval.
   Abarenicola (4 h) (weight and number of defecations)
   Axiothella (2 h) (area of core surface covered)
   Spiophanes (2 h) (weight and number of fecal rods)
4. Fresh feces were collected, dried, and weighed as a measure of fecal output per defecation.
5. Percent organic content of fresh feces was determined.
   Abarenicola
6. Percent organic content of sediment was determined at initiation and termination.
   Abarenicola (field and laboratory), *Axiothella, Spiophanes*
7. Depth of each individual's burrow was measured at termination.
   Abarenicola (field and laboratory)
8. Tube material in the cores was collected and dried and weighed at termination.
   Axiothella, Spiophanes, Pygospio

Animals were assigned by random number to treatments (control, experimental), locale (field, laboratory), block within locale, and duration type (13 or 25 days). There were 20 individuals per treatment per locale per duration type, a total of 160 individuals. The tips of the tails of the experimental individuals were ablated with a scalpel. Less than 5 mm was removed in all cases. The individuals were placed on the surfaces of their assigned cores in sea water and their burrowing times recorded. The experimental containers in the laboratory experiments were aged 1000 ml plastic beakers (11.3 cm diam. and 14.3 cm tall) filled to the rim with sediment. In the field the containers were of equal dimensions but of fiberglass windowscreen (1 mm mesh) glued together with Hot Melt Glue (Thermogrip R). Prior to transportation of the mesh cores to the field, they were wrapped with plastic to prevent loss of sediment. The plastic wrap was removed prior to implantation. Twenty-four hours after initiation the field cores were implanted in the area from which the animals had originated. A sediment core of the same size as the mesh experimental core was removed. An external sleeve held the surrounding sediment in place while the experimental core was inserted and then the sleeve was removed. The mesh edge of the experimental core protruded 1 to 5 mm above the sediment surface. Both in the field and in the laboratory the cores were arranged randomly within blocks.

The laboratory and the field cores were monitored daily for the presence of fecal castings. On days 6, 12, 18, and 24 after initiation the laboratory cores were cleared of surface feces by waving a spoon in the water above the sediment. The cores were then observed for 4 hours, and all feces were collected as they were deposited by carefully picking up the mucous-bound fecal matter with a fork and a spoon. The time of deposition of the feces was recorded. The feces were dried and ashed to determine organic content.

Both in the field and in the laboratory half of the cores were terminated on day 13 and half on day 25. At termination sediment samples were taken from a. the

sediment surface, b. the head shaft of the animal's burrow, and c. the sediment adjacent to, but not part of, the head shaft. In the field cores these samples were taken in the field immediately after removing the core from the surrounding sediment. The depth of the burrow and the condition of the individual were noted.

Axiothella *experiments*

Axiothella rubrocincta were collected in July 1982 from the mid-intertidal zone of a sand flat at False Bay. They were removed from their tubes, cleaned, and assigned by random number to a treatment (control, experimental). The tip of the tail of each experimental individual was ablated (pygidium plus one or two segments, less than 5 mm). The individuals were placed on the surface of their assigned cores and timed to complete burial.

The experimental cores were 15 cm lengths of 8 cm internal diameter PVC pipe which had been aged in sea water prior to the experiment. The cores were filled with sediment to within 1 cm of the rim of the core and placed in a Latin square design in a running sea water table. There were 10 replicates per treatment for a total of 20 cores.

The cores were monitored daily for evidence of feces. At least every other day the core surface was cleared of feces. A layer of calcium carbonate powder (less than 1 mm thick) was spread over the surface with a double screen flour duster. This provided a white background against which fresh feces could be photographed. The core was checked after one hour for feces. At two hours the cores were individually photographed using a camera with a macrolens and two strobes. The tank was drained prior to photographing to reduce reflections. The area of the fecal material on the core surface was determined from the negative with a digitizer interfaced with a computer. Such fecal areas are significantly correlated with fecal weights and volumes (MacRae, 1983). At termination a sediment sample was taken from the surface of each core for organic content analysis. Each animal was removed from its core and the sediment was sieved on a 1 mm mesh sieve to remove all tube material. The tubes were dried and weighed.

Spiophanes *experiments*

Individuals of *Spiophanes bombyx* were collected in April 1982 from an intertidal muddy sand habitat on Debidue Creek, North Inlet, Georgetown, South Carolina (33°20'N:79°10'E). Undamaged individuals were assigned by random number to a treatment (control, missing one tentacle, missing two tentacles) and a block (5). Either one or both tentacles were removed by pulling lightly on the tentacle. The individuals were then placed on the surface of their assigned cores. There were two replicates per treatment per block for a total of 30 cores. The cores were 2.8 cm diam. by 11.0 cm high plastic centrifuge tubes that had been aged in sea water. They were arranged in a randomized block design in a 36 cm by 31 cm by 18 cm deep tank in running sea water. After 12 hours the cores were transported 125 miles to Columbia, South Carolina where they were kept in the same tank in aerated sea water in an incubator at 16°C on a 12 hour day-night cycle.

Every day the core surfaces were cleared of all fecal rods. Two hours after clearing the new fecal rods were collected from the surface with a pipette, counted, dried, and weighed. At termination (13 days) a surface sediment sample was taken for organic analysis and then the core sediments were sieved on a 0.5-mm mesh sieve. The tubes were collected, dried, and weighed.

Pygospio *experiments*

Individuals of *Pygospio elegans* were collected in July 1982 from an intertidal muddy sand habitat in False Bay. Individuals were assigned by random number to a treatment (control, missing one tentacle, missing two tentacles) and a block (5). There were two replicates per treatment per block for a total of 30 cores. After assignment depending upon the treatment one or both tentacles of experimental individuals were removed by lightly pulling on the tentacle. The individual was then placed on the surface of its assigned core. The core was 2.8 cm diam. by 11.0 cm high plastic centrifuge tube that had been aged in sea water. They were arranged in a randomized block design in running sea water in a 20 cm deep sea water table. At termination (seven days) the core sediments were sieved on a 0.5 mm mesh sieve. The tubes were collected, dried, and weighed.

Statistical analyses

In all experiments except those with *Pygospio* fecal samples were taken over time from the same cores (see Table I). These were analyzed using a repeated measures analysis of variance (Winer, 1971). Several of the analyses involved nested ANOVA's (Winer, 1971; Kirk, 1982). These cases are indicated in the Results. When the data did not involve repeated measures or nested designs, a standard analysis of variance was used. When significant effects ($P < 0.05$) or strong trends ($0.05 < P < 0.10$) were indicated by the results of the analysis of variance, and the interaction terms were not significant, a Bonferroni test was used to identify differences among the treatments (Neter and Wasserman, 1974). The experimentwise error rate was 0.05. Either a Chi-square Test or a Fisher's exact test was used to compare the rates of return to defecation of control and ablated individuals of *Abarenicola, Axiothella,* and *Spiophanes* (Siegel, 1956).

Results

Abarenicola *experiments*

Burrowing times measured at initiation did not differ significantly among individuals assigned to the field and the laboratory experiments (nested ANOVA, locale, $F = 0.01$, $df = 1, 2$, $P > 0.91$). Burrowing times were also not significantly different between ablated and control individuals (nested ANOVA, treatment, $F = 0.03$, $df = 1, 2$, $P > 0.87$) nor was the interaction term of treatment and locale significant (nested ANOVA, $F = 1.14$, $df = 1, 2$, $P > .39$). Burrowing times in seconds (means and standard deviations) were as follows: field: control 119.4 (49.9), exp. 130.6 (80.4); laboratory: control 126.6 (36.4), exp. 119.1 (42.4).

As predicted, ablated individuals were slower to resume defecation than control individuals in the field as well as in the laboratory (Fig. 1). In the field a majority of ablated individuals resumed defecation within six days while in the laboratory a majority returned within eight days. Although experimental individuals in the laboratory are slower to resume defecation than those in the field, the pattern is similar (Fig. 1) suggesting that the measurements confined to laboratory populations are informative (see Table I for a summary of laboratory and field measurements). In the laboratory the proportion of control individuals defecating within the four-hour observation period was significantly greater than the proportion of experimental individuals defecating (Table II, Active) (Chi-square: 13 day: $\chi^2 = 11.66$, $df = 1$, $P < 0.001$; 25 day: $\chi^2 = 42.13$, $df = 1$, $P < 0.0001$).

In the laboratory within a four-hour period of observation ablated individuals

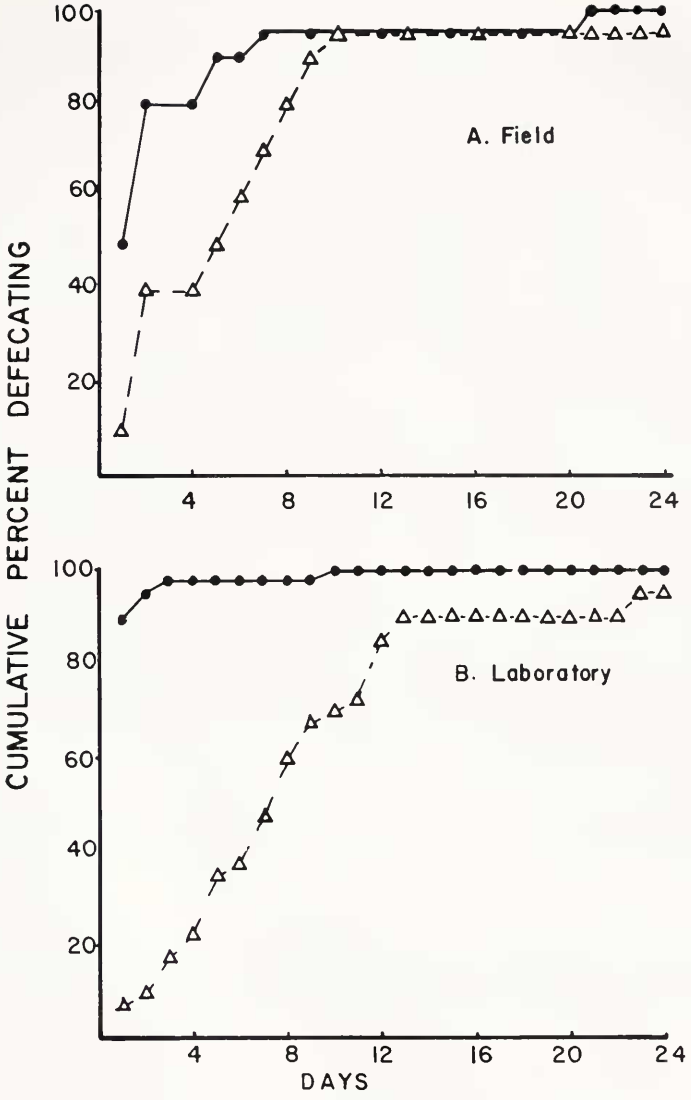

FIGURE 1. Cumulative percentage of *Abarenicola* defecating in cores in the field (A) and in the laboratory (B). Means and standard deviations of control (●) and experimental individuals (△). Days are number of days since initiation of the experiment.

defecated significantly less frequently than did the controls (Table II) (repeated measures ANOVA with individuals nested under cross of treatment and block, 13 day exp: $F = 5.55$, df = 1, 36, $P < 0.025$; 25 day exp.: $F = 15.44$, df = 1, 36, $P < 0.0001$). The number of defecations observed changed with time (significant date effect) (13 day exp.: $F = 4.37$, df = 1, 36, $P < 0.05$; 25 day exp.: $F = 4.52$, df = 3, 108, $P < 0.005$) but not as a function of treatment (date * treatment interaction effect, 13 day exp.: $F = 1.65$, df = 1, 36, $P > 0.2$; 25 day exp.: $F = 1.73$, df = 3, 108, $P > 0.16$). The lack of a significant date * treatment interaction term indicates that the significant treatment difference persists throughout the experiment (25 days). The

TABLE II

Abarenicola *experiment: number of defecations, fecal weights, and proportion of individuals defecating during four-hour periods of observation in the laboratory*

		No. def.		Fecal wt.		Active	
	Day	C	E	C	E	C	E
A.	6	1.0 (1.8)	0.2 (0.9)	.1427 (.1773)	.0098 (.0303)	.45	.10
	12	3.3 (5.0)	0.7 (3.4)	.1147 (.1371)	.0051 (.0230)	.45	.05
B.	6	2.3 (3.9)	0.5 (1.6)	.1401 (.1518)	.0232 (.0609)	.50	.15
	12	6.1 (4.8)	1.2 (3.9)	.1994 (.1460)	.0199 (.0636)	.70	.10
	18	3.6 (4.2)	0.7 (2.3)	.1568 (.1440)	.0198 (.0618)	.65	.10
	24	4.9 (4.9)	1.6 (3.6)	.1682 (.1486)	.0441 (.0966)	.70	.20

Means and standard deviations. n = 20 worms per treatment in each experiment. A. Experiment terminated on day 13. B. Experiment terminated on day 25. No. def. = number of defecations per worm per 4 hours. Fecal wt. = mean weight in grams of feces produced per worm per defecation during the 4-hour period. Active = proportion defecating within 4-hour period. C = control individuals. E = experimental individuals (ablated tail tips). Day = number of days elapsed since initiation.

ablated individuals had not yet recovered 25 days after ablation. Although the majority of the ablated individuals resumed defecation within six to eight days, frequency and amount per defecation are still below those for controls at 24 days (Table II).

The results for fecal weights are similar to those for number of defecations (Table II). The weights of individual fecal piles were significantly lower for ablated individuals than for control individuals (Table II) (repeated measures ANOVA with individuals nested under cross of treatment and block, 13 day exp.: $F = 13.24$, df = 1, 36, $P < 0.001$; 25 day exp.: $F = 34.34$, df = 1, 36, $P < 0.0001$). There were no significant differences among dates nor was the date * treatment interaction significant indicating that the treatment effect did not disappear by day 12 or 24 (date effect: 13 day exp.:

TABLE III

Abarenicola *experiment: percent organic content of sediments*

		Locale	Control	Experimental
A.	Surface			
		Field	1.3 (0.2, 13)	1.2 (0.3, 14)
		Lab	1.7 (0.2, 12)	1.8 (0.6, 17)
	Feeding area			
		Field	1.4 (0.2, 12)	1.6 (0.3, 10)
		Lab	1.7 (0.4, 15)	1.4 (0.2, 17)
	Below sediment			
		Field	1.4 (0.1, 14)	1.5 (0.3, 13)
		Lab	1.6 (0.3, 15)	1.4 (0.3, 15)
B.	Feces	Lab		
		Day 12	1.6 (0.2, 14)	1.6 (0.4, 3)
		Day 24	1.6 (0.5, 27)	1.6 (0.2, 10)

Means and standard deviations and number of replicates. Differences between controls and experimentals are not significant; see text. A. Sediments collected at termination from the core surfaces, adjacent to the head of the worm (feeding area) and at burrow depth but not adjacent to the burrow (below sediment). B. Fresh feces collected on days 12 and 24.

TABLE IV

Abarenicola *experiment: ANOVA table for percent organic content of sediments from core surfaces, the sediments adjacent to the head of the worm, and the sediments at burrow depth but not adjacent to the burrow (see Table IIIA)*

	df	MS	F	*P*
Treatment	1	5.34	0.495	.483
Sample type	2	9.40	0.871	.420
Locale	1	198.24	18.374	.0001
Treatment × locale	1	36.33	3.367	.068
Treatment × sample	2	4.84	0.448	.640
Locale × sample	2	97.79	9.064	.0001
Treatment × locale × sample	2	41.51	3.847	.023
Error	155	10.79		

F = 1.07, df = 1, 36, $P > 0.3$; 25 day exp. F = 0.83, df = 3, 108, $P > 0.45$) (date * treatment interaction: 13 day exp.: F = 0.55, df = 1, 36, $P > 0.45$; 25 day exp.: F = 0.88, df = 3, 108, $P > 0.45$). The percent organic content of the feces was not significantly different between ablated and control groups (ANOVA, treatment, F = 0.24, df = 1, 58, $P > 0.62$) nor was there a significant date effect (ANOVA, date, F = 1.93, df = 2, 58, $P > 0.15$) (Table IIIB).

The percent organic contents of the sediment surface, the feeding area, and the sediment at burrow depth were not significantly different from one another at termination (Tables III and IV, sample type not significant). There was no significant difference between ablated and control treatments (Tables III and IV, treatment not significant). There was however a significant locale effect as well as significant locale * sample and locale * sample * treatment interactions (Table IV). Depths of burrows at termination (25 days) also showed a significant locale effect but not a significant treatment effect (Table VB). Field burrows were significantly shallower than burrows made by individuals in the laboratory regardless of treatment (Table VA).

Axiothella *experiments*

The proportion of individuals defecating within the two-hour period of observation differed between the controls and the experimentals up through day six (Table VI)

TABLE V

Abarenicola *experiment: depth in cm of burrow at termination*

A.		Control	Experiment
	Field	10.75 (0.84, 18)	10.03 (1.31, 16)
	Laboratory	12.04 (0.41, 20)	12.18 (0.35, 19)

B.		df	MS	F	*P*
	Treatment	1	1.34	6.25	.130
	Treatment × locale	1	3.13	14.56	.062
	Error	2	0.21		
	Locale	1	52.39	125.98	.008
	Block within locale (Locale error)	2	0.42	0.64	.529
	Within cell error	65	0.65		

A. Means and standard deviations and number of replicates. B. ANOVA table for nested design with block nested under locale and locale crossed with treatment.

TABLE VI

Axiothella experiment: proportion of individuals that defecated during two hour observation period

Day	Control	Experimental
1	0.00	0.00
2	.80	.60
4	.90	.50
6	.70	.40
8	1.00	1.00
10	1.00	1.00
12	.90	1.00
15	.90	1.00

Number of replicates is ten per treatment for all dates. All worms in both treatments had defecated by day 4. Ninety percent of the controls and one hundred percent of the experimentals had defected by day two. Experimental individuals had their tails ablated.

(Chi-square, days 1–6, $\chi^2 = 4.05$, df = 1, $P < 0.05$; Fisher's Exact test, days 8–15, $P > 0.2$). The proportion of the sediment surface covered by feces within the two hours differed significantly among treatments and dates (Fig. 2, Table VII). The treatment * date interaction was also significant (Table VII). As is true in other maldanids (Dobbs, 1983) the activity rates of the controls as well as those of the experimental individuals appear to show a reaction to handling (Fig. 2). However the controls show significantly greater defecation activity than the experimental individuals (Fig. 2).

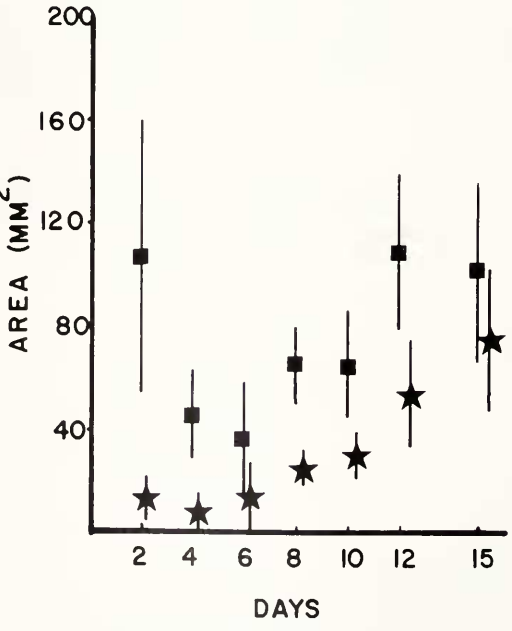

FIGURE 2. *Axiothella* experiment. Area of core surface in mm² (core area 5027 mm²) covered by feces after two hours. Ten replicates per treatment. Means and 95% confidence intervals of control (■) and experimental individuals (★). Days are number of days since initiation of the experiment.

TABLE VII

Axiothella experiment: ANOVA table for surface area of core covered by feces after two hours

	df	MS	F	*P*
Treatment	1	69154.02	24.50	.0001
Error	18	2823.05		
Date	6	12038.31	9.57	.00001
Treatment × date	6	2976.45	2.37	.0346
Error	108	1257.44		

Repeated measures design, cores nested under treatments. Ten replicates per treatment. See Figure 2.

At termination the weights of tubes collected from the cores did not differ significantly between treatments (ANOVA, $F = 0.739$, df = 1, 18, $P > 0.40$) although the mean tube weight collected in the experimental cores was less than that collected from the control cores (Table VIII). Percent organic content of the surface sediments also did not differ between treatments at termination (ANOVA, $F = 0.16$, df = 1, 18, $P > 0.69$) [means and standard deviations, controls: 1.1 (0.1), exp.: 1.1 (0.1)].

Spiophanes *experiments*

The proportion of individuals defecating during the two-hour observation period did not differ significantly between the controls and individuals missing one tentacle (Chi-square analysis, $\chi^2 = 0.894$, df = 1, $P > 0.34$) (Table IXA). The proportion of control individuals defecating was significantly different from the proportion defecating of the individuals missing two tentacles (Chi-square analysis, $\chi^2 = 15.701$, df = 1, $P < 0.0001$) (Table IXA). The proportion defecating of the individuals missing two tentacles was also significantly different from the proportion defecating of the individuals missing one tentacle (Chi-square analysis, $\chi^2 = 7.427$, df = 1, $P < 0.006$) (Table IXA). In both cases the proportion defecating of the individuals missing two tentacles was significantly lower than those for the controls or the individuals missing one tentacle (Table IXA). These differences persisted throughout at least the first seven days of the experiment (Table IXA). In all treatments the majority of the individuals resumed defecation within two days (Table IXB).

The total weight of feces produced during a two hour period differed significantly among treatments and among dates (Table X) (repeated measures ANOVA, treatment, $F = 6.27$, df = 2, 8, $P < 0.03$; date, $F = 3.37$, df = 6, 48, $P < 0.008$). The date *

TABLE VIII

Weights in grams of tubes collected at termination of the experiments

	Control	Experimental	
A.	3.072 (1.068)	2.638 (1.186)	
	Control	Missing One Tentacle	Missing Two Tentacles
B.	.1155 (.0271) a	.0835 (.0351) c	.0972 (.0241) a c
C.	.0079 (.0019) a	.0077 (.0047) a	.0068 (.0016) a

Means and standard deviations. A. *Axiothella* tubes. Ten replicates per treatment. Difference between means is not significant; see text. B. *Spiophanes* tubes. Ten replicates for control and missing two tentacle treatments, seven for missing one tentacle treatment. C. *Pygospio* tubes. Ten replicates per treatment. Differences in letters between values in a row indicate significant differences (Bonferroni *t*-test).

TABLE IX

Spiophanes *experiment: A. proportion of individuals which defecated during the two hour period of observation; B. cumulative proportion defecating*

	Day	C	1T	2T
A.	2	.90	.86	.50
	3	.70	.71	.60
	4	1.00	1.00	.50
	7	1.00	.86	.50
	9	1.00	1.00	.80
	11	1.00	.86	.80
	13	.90	.86	.90
B.	1	1.00	.60	.30
	2	1.00	1.00	.90
	3	1.00	1.00	1.00

C = control individuals, 1T = individuals missing one tentacle, 2T = individuals missing two tentacles.

treatment interaction term was not significant indicating that the treatment differences persisted throughout the 13 days of the experiment (repeated measures ANOVA, $F = 0.84$, df = 12, 48, $P > 0.61$). Bonferroni t-tests revealed that the fecal weights for the individuals missing two tentacles were significantly different from those of the control and the individuals missing one tentacle but that the values for the individuals missing one tentacle were not significantly different from those of the

TABLE X

Spiophanes *experiment: total weight of feces (grams) produced during two-hour periods by single individuals*

Day	C	1T	2T	Date Means
2	.0017 (.0012, 10)	.0010 (.0006, 7)	.0006 (.0010, 10)	.0011 a
3	.0014 (.0011, 10)	.0010 (.0009, 7)	.0010 (.0010, 10)	.0013 a
4	.0016 (.0007, 10)	.0018 (.0008, 7)	.0008 (.0010, 10)	.0012 a
7	.0019 (.0005, 10)	.0015 (.0008, 7)	.0008 (.0009, 10)	.0013 a d
9	.0017 (.0003, 10)	.0018 (.0007, 7)	.0013 (.0008, 10)	.0016 a d e
11	.0022 (.0004, 10)	.0018 (.0009, 7)	.0014 (.0008, 10)	.0018 b d e
13	.0017 (.0008, 7)	.0024 (.0009, 6)	.0018 (.0008, 10)	.0019 b e
Treatment Means	.0017 a	.0016 a	.0011 b	

C = control individuals, 1T = missing one tentacle individuals, 2T = missing two tentacle individuals. Means and standard deviations and number of replicates per date. Factor level means of treatments and dates. Differences in lower case letters indicate significant differences among factor level means (Bonferroni t-test).

controls (Table X). Mean fecal weights for days 2 to 4 were significantly different from those for days 11 and 13. Days seven and nine were intermediate (Table X).

The number of fecal rods produced during a two-hour period also differed significantly among treatments and among dates (Table XI) (repeated measures ANOVA, treatment, $F = 4.83$, $df = 2, 8$, $P < 0.05$; date, $F = 3.24$, $df = 6, 48$, $P < 0.01$). As for total fecal weight the date * treatment interaction term was not significant indicating that the treatment differences persisted throughout the 13 days of the experiment (repeated measures ANOVA: $F = 1.53$, $df = 12, 48$, $P > 0.14$). Bonferroni t-tests revealed that the mean numbers of fecal rods differed significantly between the control individuals and the individuals missing two tentacles. Values for individuals missing one tentacle, however, were not significantly different from those for individuals missing two tentacles or from values for control individuals (Table XI). Mean numbers of fecal rods for days 2 through 7 were significantly different from those for days 9, 11, and 13 (Table XI).

At termination the tubes in the cores were collected, dried, and weighed. The ANOVA revealed no significant differences at the 0.05 level although the treatment effect had a probability of 0.061 (Table XII). A Bonferroni t-test showed that the control cores had significantly greater total tube weights than the cores with individuals missing one tentacle (Table VIIIB). Total tube weights were not significantly different between cores with control individuals and cores with individuals missing two tentacles. Cores with individuals missing two tentacles were also not significantly different from those with individuals missing one tentacle (Table VIIIB). At termination percent

TABLE XI

Spiophanes *experiment: total number of fecal rods produced during two-hour periods by single individuals*

Day	C	1T	2T	Date Means
2	3.0 (2.2, 10)	2.4 (2.6, 7)	1.1 (1.4, 10)	2.1 a
3	2.2 (1.8, 10)	1.1 (1.3, 7)	1.5 (1.5, 10)	1.8 a
4	3.0 (1.8, 10)	2.7 (1.0, 7)	1.0 (1.4, 10)	2.0 a
7	3.6 (1.6, 10)	2.3 (1.6, 7)	1.2 (1.3, 10)	2.1 a
9	3.1 (1.7, 10)	2.3 (2.2, 7)	3.1 (2.6, 10)	3.1 b
11	4.4 (1.6, 10)	3.1 (1.9, 7)	2.5 (1.6, 10)	3.4 b
13	2.7 (2.0, 7)	4.2 (2.6, 6)	3.7 (2.6, 10)	3.5 b
Treatment Means	3.2 a	2.6 a b	2.0 b	

C = control individuals, 1T = individuals missing one tentacle, 2T = individuals missing two tentacles. Means and standard deviations and number of replicates per treatment per date. Factor level means of treatments and dates. Differences in letters indicate significant differences among factor level means (Bonferroni t-test).

TABLE XII

Spiophanes *experiment: ANOVA table for weight of tubes*

	df	MS	F	*P*
Treatment	2	2039.87	3.56	.061
Block	4	769.48	1.34	.310
Treatment × Block	8	1235.42	2.15	.111
Error	12	573.19		

Two-way ANOVA with treatment crossed with block. See Table VIII.

organic content of surface sediments did not differ significantly among treatments (ANOVA, $F = 2.66$, $df = 2, 24$, $P > 0.09$).

Pygospio *experiments*

Pygospio is smaller than *Spiophanes* so no attempt was made to measure activity other than by weight of tubes collected at termination. Tube weights did not differ significantly among the treatments (Table VIIIC) (ANOVA, $F = 0.231$, $df = 2, 12$, $P > 0.50$).

DISCUSSION

Biogenic alteration of sediments is known to affect the flux of compounds into and out of interstitial water (Aller, 1978, 1982; McCaffrey *et al.*, 1980; Waslenchuk *et al.*, 1983), the ability of sediments to be resuspended (Rhoads and Young, 1970; Rhoads, 1974; Myers, 1977a, b; Rhoads *et al.*, 1978) and the physical structure of the sediment (Rhoads, 1974; Myers, 1977a; Rhoads and Boyer, 1982). Indirect interactions among infauna often are mediated by such biogenic alterations of the sediment. The concept of 'trophic amensalism' (Rhoads and Young, 1970) and its subsequent modifications (Woodin, 1976; Brenchley, 1981) are descriptions of how biogenic alteration of sediments by the movements and feeding and defecation of infauna affects the survivorship and/or emigration of infauna (Weinberg, 1979; Brenchley, 1981, 1982; Wilson, 1981) as well as the growth rates of individuals (Rhoads and Young, 1970).

The rate at which infauna modify the sediments is usually described as being a function of their species, size, and density as well as physical variables such as temperature (Mangum, 1964; Rhoads, 1967, 1974; Cadee, 1976; Kudenov, 1982; Dobbs, 1983; Thayer, 1983). It may also be a function of their health as that affects their activity. Primary dietary components of juvenile flatfish often are the tails and tentacles of worms and the siphons of bivalves (Macer, 1967; Trevallion *et al.*, 1970; Braber and deGroot, 1973; Kuipers, 1977; deVlas, 1979a); regenerating worms and bivalves are common in infaunal samples (Mangum, 1964; deVlas, 1979b; Wilson, 1979).

The results of these experiments demonstrate that tissue loss affects the activities of three polychaetes, *Abarenicola, Axiothella,* and *Spiophanes.* Defecation frequency and fecal amounts were negatively affected in all three species. Ablated individuals of *Abarenicola* were significantly slower to return to defecation after the initiation of the experiment than controls (Fig. 1); they had significantly fewer defecations per time interval than controls (Table II), and their fecal piles were significantly lighter in weight than those of control individuals (Table II). In *Axiothella* the proportion of control individuals defecating was larger than that of the experimental individuals

(Table VI) and the amount of the core surface covered by feces was significantly greater in the control cores (Table VII, Fig. 2). In *Spiophanes* loss of both tentacles significantly affected the proportion of individuals defecating, the total weight of feces, and the total number of fecal rods (Table IX, X, and XI); loss of one tentacle did not significantly affect these parameters. Loss of one tentacle did significantly affect the weight of tubes produced (Table VIIIB).

Some measurements were not significantly affected by tissue loss. In none of the experiments was percent organic content of sediments or feces affected (Tables III and IV). Ablated individuals of *Abarenicola* were not significantly different from control individuals in burrowing time at initiation and depth of burrow at termination (Table V). In the experiments with *Axiothella* and *Pygospio* total tubes collected at termination did not differ significantly in weight between ablated and control individuals (Table VIIIA and VIIIC).

If organisms have important influences on the chemical alteration of sediments (Aller, 1978, 1982), the physical structure of the sediments (Rhoads, 1974), and the rate of resuspension of sediments (Rhoads and Young, 1970), then any process that changes the rate at which sediment modification occurs is of interest. Tube building and defecation are two of the activities of infauna that affect sediment properties (Myers, 1977a, b; Rhoads *et al.*, 1978; Eckman, 1979, 1983; Eckman *et al.*, 1981). These experiments indicate that small amounts of tissue loss affect the rates of these activities. Both the literature on the contents of fish guts (Edwards and Steele, 1968; Braber and deGroot, 1973; Kuipers, 1977; deVlas, 1979a) and the data from static samples of infauna (Mangum, 1964; Ronan, 1975; Wilson, 1979; Woodin, 1982) indicate that such losses are common in natural populations. Models of biogenic alteration of sediments need to consider the implications of the period of relative inactivity of individuals suffering tissue losses. Rates of sediment modification measured on intact animals in the laboratory may grossly overestimate activities in field populations exposed to browsing predators.

The three polychaete species used in this study belong to three families that are very common in the intertidal zone and along the continental shelves of the Atlantic and Pacific Oceans. Arenicolids are often the most common large infaunal organism in samples from shallow water on the European coast (Beukema and deVlas, 1979) as well as elsewhere (Hobson, 1967). Both arenicolids and maldanids increase the rate at which sediment turns over (Hobson, 1967; Rhoads, 1967; Cadee, 1976; deVlas, 1979b). Both also appear to affect the local composition of the infauna through their effect on the sediment (Wilson, 1981; Weinberg, 1979). Most members of both families feed at depth and defecate on the surface. For these organisms it is this defecation onto the sediment surface that alters the local sediment turnover rates and affects the rest of the infauna. Spionids, although much smaller, are very common and are known to change the stability of sediments by their tube-building activities (Featherstone and Risk, 1977). The tube-building activities of maldanids can also significantly affect sediment properties (Rhoads, 1974; Featherstone and Risk, 1977). The results of these experiments indicate that small amounts of tissue loss will dramatically alter rates of sediment alteration. Clearly, in attempting to assess the importance of biogenic sedimentary change in determining the composition of the local assemblage, as well as the chemical and physical structure of the sediment, it is necessary to know the activity rates of the individuals determining biogenic sediment turnover rates. If the rates of recovery from tissue loss indicated in this paper are generally true, sediment turnover rates calculated from laboratory and/or field observations on intact individuals may be incorrect by an order of magnitude or more depending upon the frequency of tissue loss in the field.

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